Maturation of spatial-frequency and orientation selectivity of primary visual cortex

U. Shahani, V. Manahilov, and D.L. McCulloch

Department of Vision Sciences, Glasgow Caledonian University, City Campus, Cowcaddens Road, Glasgow G4 0BA, Scotland

1 Introduction

Remarkable changes of spatial vision occur during the first few months in human life. Maturation of spatial vision is due to morphological and biochemical development along visual pathways from retina to cortex. It has been hypothesised that newborn vision is mediated by subcortical processes and that a significant amount of human cortical development emerges postnatally [1,2]. One of the features of the development of the primary visual cortex is the development of cortical channels with bandpass spatial-frequency and orientation tuning characteristics. These channels are thought to mediate human adult spatial vision. They have been found in the primary visual cortex, but not at the earlier stages in the visual pathway (retina and LGN) [3,4].

Using a behavioural-looking technique combined with pattern masking, evidence was found for multiple bandpass spatial-frequency channels in 12-week-old but not 6-week-old infants [5]. Sutter at al. [6] studied pattern adaptation effects on steady-state visually evoked potentials (VEPs) and have suggested that spatial-frequency selective channels exist at the age of 3 weeks. Records of orientation-specific VEPs have demonstrated that the postnatal onset of orientation-specific responses is about 6 weeks after birth [7]. However, this study used large orientation shift and the magnitude of the orientation selectivity was not examined. Thus, it is clear that young infants develop selectivity in both orientation and spatial frequency domains but maturation of the tuning characteristics of each domain remains unclear and comparisons between them are not possible. Moreover, previous studies have used steady-state VEPs employing high temporal frequency of stimulation which may have been crucial in determining the onset of orientation and spatial-frequency properties of visual cortex.

In the present work, we studied simultaneously the development of spatial-frequency and orientation selective mechanisms in the striate cortex of human infants and compared their tuning characteristics with those in the adult. To this end we measured the effect of an adapting grating on the VEPs recorded in response to a test grating as a function of the difference between the spatial frequency and orientation of both stimuli. Monopolar VEPs were recorded simultaneously form three electrodes placed on the scalp above the striate cortex. Laplacian analysis of the VEPs was used which is known to attenuate the contribution from extrastriate cortical areas and reflect mainly the activity of the striate visual cortex [8].

2 Methods

2.1 Stimuli

The stimuli were circular sinusoidal gratings generated with a Pentium computer and displayed on a monitor with 256 grey levels and 12 bit luminance resolution. The screen with a mean luminance of 30 cd/m^2 was surrounded by a large screen (100 x 100 cm) illuminated so as to approximate the display in luminance and hue. The viewing distance was 35 cm at which the stimulus subtended 40 deg in diameter at the subject's eyes. A stimulus cycle consisted of an adaptation period of 400 ms, an inter-stimulus interval (varied randomly between 100 and 200 ms), a prestimulus interval of 30 ms, a test-stimulus presentation of 50 ms and a blank interval of 350 ms (Fig. 1). The test stimulus was a horizontal grating having a spatial frequency of 0.4 c/deg and contrast of 0.45. The adapting stimulus was a high-contrast grating (0.9), which varied in spatial frequency (0.14 – 1.12 c/deg) and orientation (0^0 to 45^0).

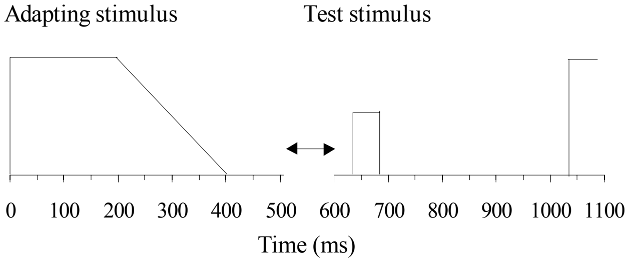

Figure 1: *Schematic diagram of a stimulus cycle.*

To minimise afterimages of the adapting gratings: (1) they were shifted 1 cycle to the left and right at 3 Hz and (2) the adapting-stimulus offset was a linearly decaying function of stimulus contrast.

2.2 VEP recording

EEG was recorded simultaneously from three monopolar derivations: Oz, O1 and O2. The reference electrode was placed on the left ear and the ground electrode on the right ear. The raw EEG was amplified, bandpass filtered between 0.3 and 100 Hz and then subjected to 12-bit digitisation at 400 Hz. VEPs were obtained by averaging at least 10 artifact-free EEG sweeps. Laplacian derivations were calculated on-line as 2 times the potential of the middle electrode (Oz) minus the sum of the potentials of the surrounding electrodes (O1 and O2). The amplitude of the first prominent component of the Laplacian derivations was measured from the averaged baseline value 30 ms before the stimulus onset to the corresponding peak.

2.3 Subjects

Four adults and two infants (corrected ages of three to eleven weeks) were tested in multiple sessions (Fig. 2).

Figure 2: *Subject MM during an experiment at 6-week age.*

3 Results

3.1 Laplacian analysis

The Laplacian derivation of the VEPs (Fig. 3, bottom curves) consisted of a positive component (P1), which was not always recognisable in the monopolar derivations (Fig. 3 upper three curves). This component reflects the early part of the monopolar responses whose generators are located in the striate cortex.

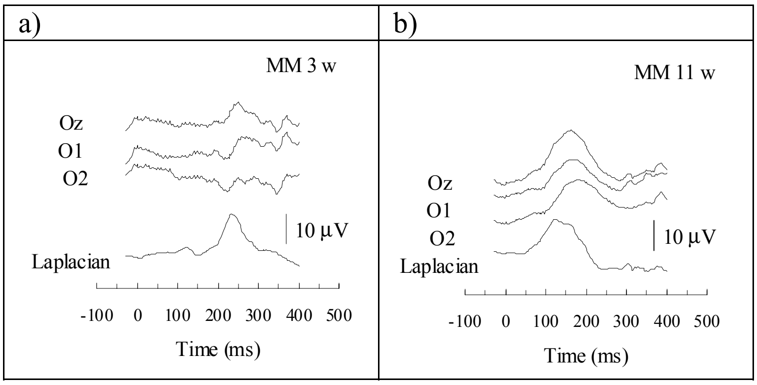

Figure 3: *Examples of monopolar VEPs (upper three curves) and Laplacian derivations (bottom curves). Data for subject MM at age of 3 weeks (a) and eleven weeks (b).*

3.2 Latency of P1 Laplacian component

In the absence of the adapting pattern, the peak latency of the positive Laplacian component P1 was about 240 ms at three weeks of age and approached adult values of about 120 ms at eleven weeks (Fig. 4).

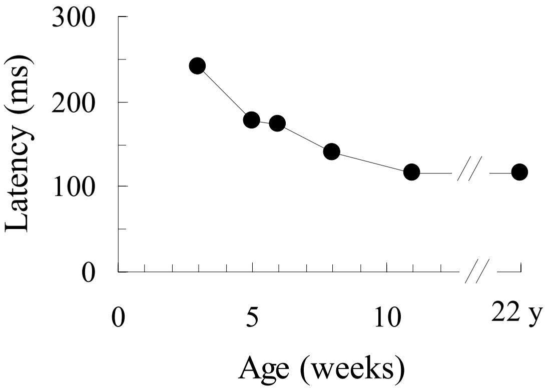

Figure 4: *Peak latency of P1 Laplacian component as a function of age for one infant subject and a representative adult.*

3.3 Effects of spatial-frequency adaptation

When the adapting stimulus and test stimulus were horizontal gratings, pattern adaptation effect on the P1 amplitude depended on the spatial frequency of the adapting grating (Fig. 5)

The maximal effect of pattern adaptation was observed when both stimuli had the same spatial frequency and orientation. The half-height bandwidth of spatial-frequency tuning characteristics was about 2 octaves regardless of the subject's age (Fig. 6).

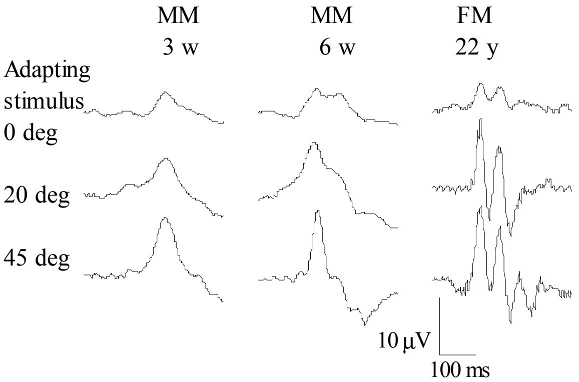

Figure 5: *Laplacian waveforms illustrating the effect of the spatial frequency of the adapting grating on the P1 amplitude elicited by a horizontal grating of 0.4 c/deg. Data from a representative infant at 3 weeks (left column) and 6 weeks (middle column) of age and a representative adult at 22 years of age (right column).*

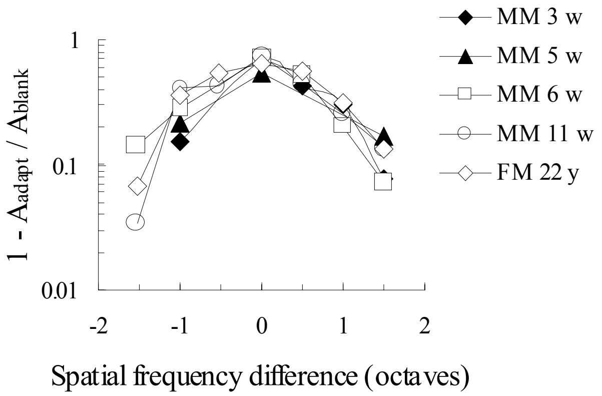

Figure 6. *Relative changes in P1 amplitude to a horizontal test stimulus of 0.4-c/deg spatial frequency, produced by a horizontal adapting grating of variable spatial frequency. The ordinate is the difference between P1 amplitude to the test grating obtained without and with the adapting grating, expressed as a percentage of the P1 amplitude to the test stimulus alone. The abscissa represents the difference between the spatial frequencies of the test and adapting gratings in octaves. Data for subjects at different ages.*

3.4 Effects of orientation adaptation

The effect of orientation difference between the test and adapting stimuli of 0.4 c/deg on the Laplacian response is illustrated in Fig. 7.

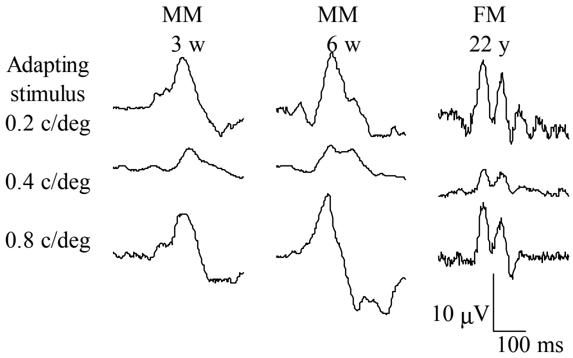

Figure 7: *Laplacian waveforms illustrating the effect of the orientation of the adapting grating on the P1 amplitude elicited by a horizontal test grating. Both stimuli have a spatial frequency of 0.4 c/deg. Data from a representative infant at 3 weeks (left column) and 6 weeks (middle column) of age and a representative adult at 22 years of age (right column).*

The half-height bandwidth of the orientation-tuning curve was about 40^0 at three weeks of age. However, from six weeks onwards this quantity decreased to about 20^0, which is similar to the half-height bandwidth of the orientation-tuning curve of adults (Fig. 8).

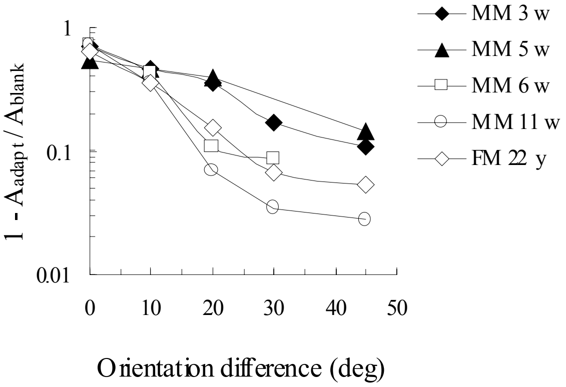

Figure 8. *Relative changes in P1 amplitude to a horizontal test stimulus of 0.4-c/deg spatial frequency, produced by a 0.4-c/deg adapting grating of variable orientation. The ordinate is the difference between P1 amplitude to the test grating obtained without and with the adapting grating, expressed as a percentage of the P1 amplitude to the test stimulus alone. The abscissa represents the difference between the orientation of the test and adapting gratings. Data for subjects at different ages.*

4 Discussion

The present study confirmed previously reported findings [8] that Laplacian analysis allows for the selective recording of activity of striate cortex. It was shown that Laplacian derivation of the VEP to gratings of low spatial frequency consisted of a positive component which was not always recognisable in the monopolar derivations. The Laplacian derivation is insensitive to contributions of remote generators like those due to eye movements. Moreover, the signal-to-noise ratio of the Laplacian derivation of the VEP is higher than that of the monopolar VEP recording.

The observed changes in the latency of the P1 Laplacian component are in line with other studies of VEP latency in infants [9]. We have found that during the period of maturation of the visual pathways, both spatial-frequency and orientation selectivities are present and show substantial maturity at three weeks postnatally, but the time course of development appears to be different. The results imply that separate cortical processes underlie maturation of the spatial-frequency and orientation selective mechanisms in visual cortex. One might suggest that the receptive fields of neurones in infant striate cortex are narrowly tuned in spatial frequency at three weeks of age but orientation tuning is less mature. It may be that receptive fields elongate substantially as the infant's age increases from three to six weeks. This suggestion may explain the narrowing of the orientation-tuning curves.

Biomagnetic techniques combined with the approach used in the present study may be useful in studying the maturation of spatial vision in the human striate cortex.

Acknowledgements

This work was supported by a Royal Society Research Grant to V.M.

References

1. G.W. Bronson, "The postnatal growth of visual capacity", *Child Development,* **45**, 873, 1974.
2. J. Atkinson, " Human visual development over the first six months of life. A review and a hypothesis", *Human neurobiology*, **3**, 61, 1984.
3. D.H. Hubel ,and T.N. Wiesel, "Receptive fields, binocular interaction and functional architecture in the cat's visual cortex", *Journal of Physiology* (London), **195,** 215, 1962.
4. F.W. Campbell, G.F. Cooper and C. Enroth-Cugell, "The spatial selectivity of the visual cells of the cat*", Journal of Physiology* (London), **203***,* 237, 1969.
5. M.S. Banks, B.R. Stephens, and E.E. Hartmann, "The development of basic mechanisms of pattern vision: Spatial frequency channels", *Journal of Experimental Child Psychology*, **203,** 237, 1985.
6. P.S. Suter, S. Suter, J.S. Roessler, K.L. Parker, C.A. Armstrong, and J.C. Powers. "Spatial-frequency-tuned channels in early infancy: VEP evidence", *Vision Research*, **34**, 737, 1994.
7. O.J. Braddick, J. Wattam-Bell, and J. Atkinson, "Orientation-specific cortical responses develop in early infancy", *Nature*, **320**, 617, 1986.
8. V. Manahilov, F.C. Riemslag, and H. Spekreijse, "The Laplacian analysis of the pattern onset response in man", *EEG and Clinical Neurophysiology*, **82**, 220, 1992.
9. D.L. McCulloch, H. Orbach, and B. Skarf, "Maturation of the pattern-reversal VEP in human infants: a theoretical framework", *Vision Research*, **39,** 3673, 1999.